Tools and Technology Article

Estimating Abundance From One-Dimensional Passive Acoustic Surveys

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ABSTRACT Conventional distance sampling, the most-used method of estimating animal density and abundance, requires ranges to detected individuals, which are not easily measured for vocalizations. However, in some circumstances the sequential pattern of detection of vocalizations along a transect line gives information about the range of detection. Thus, from a one-dimensional acoustic point-transect survey (i.e., records of vocalizations detected or not detected at regularly spaced listening stations) it is possible to obtain a useful estimate of density or abundance. I developed equations for estimation of density for one-dimensional surveys. Using simulations I found that for the method to have little bias when both range of detection and rate of vocalization need to be estimated, stations needed to be spaced at 30–80% of the range of detection and the rate of vocalization should be >0.7. If either the range of detection or rate of vocalization is known, conditions are relaxed, and when both parameters are known the method works well almost universally. In favorable conditions for one-dimensional methods, estimated abundances have overall errors not much larger than those from conventional line-transect distance sampling. The methods appeared useful when applied to real acoustic data from whale surveys. The techniques may also be useful in surveys with nonacoustic detection of animals. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):1000–1009; 2009)

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Distance sampling is the most frequently used method of assessing populations of wild animals (Buckland et al. 2004). In distance sampling, the primary data are records of individuals (or clusters of individuals) detected during continuous transects or at point samples together with an estimate of their ranges. These ranges permit estimation of coverage of the survey and, thus, convert the detection rate into estimates of density and population size (Buckland et al. 2001).

In distance sampling, detection of individuals or clusters is potentially by any sensory mode although visual detection overwhelmingly predominates, even though many species are more readily detected acoustically than visually. For such species, acoustic surveys (sometimes combined with visual methods) frequently provide data to plot distributions and examine trends in abundance with time and environmental variables (Jaquet and Whitehead 1996, Norris et al. 1999, Nichols et al. 2009), but estimates of density or population size are much rarer. There are several reasons for the rare use of distance-sampling methodology in acoustic surveys, but probably most significant are the difficulties of assigning vocalizations to particular animals and estimating the range to the vocalizing animals (Nichols et al. 2009). These steps are generally harder for acoustic cues than with visual detection. A few techniques are available for estimating effective acoustic detection range, particularly for cetaceans, but these techniques generally need quite sophisticated equipment or processing of the acoustic data (e.g., Leaper et al. 2000, Barlow and Taylor 2005, Nichols et al. 2009).

A common form of acoustic survey is to record whether vocalizations are detected at regular stations along a transect line. Because ranges to detected animals are usually not recorded, such survey data are not typically used for density or abundance estimation. However, the sequential pattern of detections of vocalizations potentially gives information about the range of detection. The idea is that if the distance between listening stations along a transect line is less than the range of detection, then the rate at which detections follow one another permits estimation of the detection range. Thus, my goal was to determine the circumstances in which it may be possible to obtain a useful estimate of density or abundance from a one-dimensional acoustic point-transect survey without sophisticated collection or processing of acoustic data (e.g., series of bearings to particular vocalizers). My specific objectives were to 1) derive equations that estimate detection range, probability that an individual is vocalizing, and density from such survey data, 2) investigate the circumstances under which these estimates have little bias, 3) compare expected errors of one-dimensional methods with those from conventional 2-dimensional distance sampling in a situation where both are feasible, 4) illustrate use of the methods on real acoustic transect data, and 5) suggest general protocols for their use.

METHODS

A Model and 4 Methods

I assumed that an acoustic survey consisted of a transect line (not necessarily perfectly straight) with listening stations regularly spaced at d distance units. There was a record for each station as to whether vocalizations were detected, not the number of vocalizers. Presence–absence data is simpler to collect in the field and has been the subject of technical development in related applications (e.g., estimation of abundance from repeated presence by Royle and Nichols 2003).

I assumed that individuals were randomly and independently distributed at a density of α/unit^2 and could be detected within a range of r units. Individuals produced audible (to listeners within range r) sounds with probability μ during any listening. Probabilities were uncorrelated among listening stations if an individual was within audible range for ≥ 2 stations. As in conventional line-transect

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distance sampling, I assumed individuals did not move. Therefore, density of vocalizers is $\alpha \times \mu$ per unit area and probability that ≥ 1 vocalizers were detected at a station is

$$1 - e^{-\alpha\mu\pi r^2} \quad (1)$$

Thus, if vocalizations were heard at a proportion of p stations, an estimate of density is

$$\hat{\alpha} = -\mathrm{Log}(1 - p)/\mu\pi r^2 \quad (2)$$

Using equation 2 I can estimate density if I know μ and r (method A).

If I do not know μ, but know r, then the rate at which vocalizations were detected at pairs of consecutive stations gives information about μ. For instance, if there were stations without detected vocalizations and d is much less than r, then a station at which vocalizations are detected is usually followed by another, which suggests that μ is near 1.0, whereas few consecutive records of vocalizations suggests that μ is low. More formally, we can estimate μ from (Appendix, eq A5):

$$\hat{\mu} = \frac{1 - \mathrm{Log}\left(1 - \dfrac{h}{1-p}\right) \Big/ \mathrm{Log}(1-p)}{1 - K} \quad (3)$$

where K is the proportion of the area covered by listening at a station that is not covered at another station d units away:

$$K = 1 - 2\left\{\mathrm{acos}\,[d/2r] - [d/2r]\sqrt{\left[1 - (d/2r)^2\right]}\right\} \Big/ \pi \quad (4)$$

and h is the rate that vocalizers are detected at a station but not at the subsequent station. With known r and estimated μ (eq 3), I can estimate density (eq 2; method B).

Similarly, I can estimate r if I know μ, because (equating K from eqs 3 and 4):

$$1 - 2\left\{\mathrm{acos}\,[d/2r] - [d/2r]\sqrt{\left[1 - (d/2r)^2\right]}\right\} \Big/ \pi = 1 - \frac{1 - \mathrm{Log}\left(1 - \dfrac{h}{1-p}\right) \Big/ \mathrm{Log}(1-p)}{\mu} \quad (5)$$

I can solve numerically for r. With known μ and r (eq 5), I can estimate density (eq 2; method C).

Finally, if I know neither r nor μ, a third piece of empirical information, the rate of hearing individuals at a station but not at the 2 subsequent stations, q, becomes useful. The expected value of q is (Appendix, eq A6):

$$\hat{q} = e^{\alpha\mu(\mu - K\mu - 2)}\left[1 - e^{-\alpha\mu[(1-\mu+K\mu)^z + \mu K(1-K)]}\right] \quad (6)$$

I choose a value of K such that, when I use equation 3 to estimate μ, and I enter these values into equation 6, then they satisfy equation 6. Then, I can estimate r by numerically solving equation 4 and so obtain an estimate of density (eq 2; method D).

Testing Methods and Assumptions

To test the ability of methods A–D to estimate density, I simulated survey data using the package MATLAB (The Mathworks, Natick, MA). The routine randomly placed individuals at a density of α per unit area over a study area. It arranged a sequence of N listening stations spaced at d units along a linear transect within the study area, all $\geq r$ units from the boundary. At each station, the routine recorded all individuals within a radius of r as detected with independent probabilities μ and individuals further than r as not detected. It kept a record of whether any individual was detected at each station (not how many individuals were detected). Using these data, the routine estimated the density of individuals by the 4 methods: 1) assuming both r and μ are known (using eq 2), 2) assuming r (but not μ) is known (using eqs 2–4), 3) assuming μ (but not r) is known (using eqs 2 and 5), and 4) with no knowledge of r and μ (using eqs 2, 4, and 6). Setting, without loss of generality, $r = 10$ units, I carried out 100 simulated transects with all combinations of:

$\alpha = 0.01/\text{unit}^2$, $0.001/\text{unit}^2$, $0.0001/\text{unit}^2$ (giving probabilities of having ≥ 1 individual within audible range at a listening station of 0.96, 0.27, and 0.03, respectively);

$\mu = 0.2, 0.4, 0.6, 0.8, 1.0$;

$d = 2, 4, 7, 12$ units (giving overlap between coverage at adjacent stations of 87%, 75%, 56%, and 28%, respectively; $1 - K$ from eq 4);

$N = 100, 300, 1{,}000$ stations (simulating short, medium, and long transects, respectively).

Thus there were 14,400 simulated transects. For each combination of input parameters, I calculated the bias in each estimate of density, difference between the mean (over the 100 replicates) estimate of density, $\hat{\alpha}$, and its real value α, as a proportion of α: $(\hat{\alpha} - \alpha)/\alpha$. I also recorded the number of simulations in which there was a failure of the estimation methodology (for instance because of failure to solve eqs 5 or 6).

The one-dimensional acoustic survey methodology I developed makes some assumptions. I examined effects of departures from these assumptions by introducing such departures into data sets for which the methodologies otherwise appeared to work well. So, in this part of the analysis, $\alpha = 0.001$, $\mu = 0.9$, $d = 5$, $r = 10$, and $N = 300$. I made 100 runs with each of the following variations introduced into the model. 1) The stations were not evenly spaced, which I modeled by moving each station by a normally distributed amount with mean zero and standard deviation $0.2d$ along the transect line. 2) The range of audibility varied between individuals, because, for instance, they had different source levels, which I modeled by having the range of audibility among individuals varying using a normal distribution with standard deviation $0.2r$ (where r is the mean range of audibility). 3) The range of audibility varied among stations, because of, for instance, different background noise or transmission conditions. I modeled this by having the range of audibility among stations varying using a normal distribution with standard deviation $0.2r$ (where r is the mean range of audibility). 4) The range of audibility varied for each station–individual pair, because of combinations of factors such as those considered in 2 and 3 (above), or directionality in the signal strength for individuals with changing orientations. I modeled this by having the range of audibility among station–individual pairs varying using a normal distribution with standard deviation $0.2r$ (where r is the mean range of audibility). 5–6) Densities of individuals were nonuniform. I modeled 2 variants. In the first (5), density of individuals increased linearly from zero to twice the mean density along the transect line. In the second (6), density of individuals increased linearly from half the mean density to 1.5 times the mean density along the transect line. 7–8) Individuals avoided one another, which I modeled by allowing no pairs of individuals to be closer to one another than r (variant 7) or $r/2$ (variant 8). 9) Individuals were attracted to one another, which I modeled by allowing no individual to be further from all other individuals than $5r$ units. 10) Probability of vocalizing at different stations was not independent, which I modeled by giving each individual a different probability of vocalizing. Probabilities were uniformly distributed between $2\mu - 1$ and 1, giving a mean value of μ.

If there exists a method of estimating the range to a vocalizing individual, then conventional (i.e., 2-dimensional) distance-sampling surveys (as described by Buckland et al. 2001), as well as my one-dimensional surveys, are possible. To obtain an indication of relative efficiencies of the methods, I used both on simulated data with $\alpha = 0.001$, $\mu = 1.0$, $d = 5$, $r = 10$, and $N = 300$. Unlike the tests for departures from assumptions, these simulations used $\mu = 1.0$, because conventional distance sampling makes this assumption [technically, $g(0) = 1$]. I made 1,000 simulation runs both with fixed r, as well as with r varying among individuals (variant 2 above). For each simulated data set, I made estimates of density using the one-dimensional methodology with known μ (method C), as well as using Distance 5.0 software (Thomas et al. 2006). In the latter analyses, with fixed r the fitted detection function was the uniform model plus cosine adjustments. For the data sets produced using variable r both half-normal and hazard-rate models were fitted with cosine adjustments. I calculated Akaike's Information Criterion (AIC) for each and selected the model with the lower, better AIC (see Buckland et al. 2001). I assumed that perpendicular distances from the transect line to detected vocalizers were recorded accurately. In each case the mean deviation from true density (as a proportion of input density) indicated bias, and the coefficient of variation of density estimates from different simulations indicated precision.

To illustrate the use of one-dimensional survey methods, I used an acoustic transect across the southern Sargasso Sea between 33°41.5′N 57°4.4′W (29 Feb 2008, 2000 hr local time) and 17°8.7′N 61°33.9′W (7 Mar 2008, 1730 hr local time) from a 12.5-m sailing vessel. Every half-hour a towed hydrophone was monitored for about 1 minute and presence or absence of humpback whale (*Megaptera novaeangliae*) song and sperm whale (*Physeter macrocephalus*) clicks noted. There were 332 listening stations spaced at a mean of 5.88 km (CV = 0.16; calculated using Global Positioning System records).

RESULTS

Limits of Methodologies

The 4 methods had distinctive ranges of effectiveness and bias (Figs. 1–4, and additional simulations not shown). Estimation of density using equation 2 when both r and μ were known (method A) was virtually unbiased under any of the conditions examined (Fig. 1). However, there were a few problems with high densities of vocalizers and rates of vocalization when vocalizations were detected at all stations, which caused equation 2 to produce infinite estimates. When μ, but not r, was unknown and needed to be estimated (method B), estimation of density had little bias under the following conditions (Fig. 2): μ was not too small (approx. >0.5), so that individuals within range were usually detected; d was not too large (approx. $<r$), so that there was a reasonable chance that an individual detected at one station would be detected at the next; and there was sufficient information to give a reasonable estimate of h, so that there were ≥ 5 consecutive pairs of stations at which vocalizations were detected and ≥ 5 consecutive pairs at which they were not. The data point in Figure 2 produced by runs with parameters $\mu = 0.8$, $d = 4$, $\alpha = 0.01$, $N = 300$, showing a relative bias of about -0.8 seems to be an anomaly, because I have been unable to replicate this value. In 10 replicates, each with 100 runs, using these parameters, mean relative biases ranged +0.1 to +0.5. Method C, when μ but not r was known, only seemed to work well consistently at high μ (approx. >0.7; Fig. 3). There was also bias when little information was available or with close spacing of stations ($d < r/2$). With no knowledge of r or μ (method D), estimation of density was only unbiased with $d = 3$–8 units (Fig. 4), and so a spacing of stations of 30–80% of the range of detection. Given d within this range, there was little bias at high μ, but as μ decreased below 0.7, bias increased and the estimation algorithm was more likely to fail.

I investigated departures from assumptions of the model on estimates of density using a set of parameters for which all 4 methods showed little bias when the assumptions held. Most departures produced little bias in estimates of density (Table 1), and there were no failures in the estimation procedure in these runs. However, when stations varied in their detection range, density was overestimated unless r and μ were known. In contrast, if density varied substantially between parts of the survey, then the methods, especially those that estimated r or r and μ, underestimated overall density. When individuals avoided one another, then the methods, which assume independent positions, overestimated density.

In the comparison between one-dimensional acoustic survey and conventional 2-dimensional distance sampling, the one-dimensional survey seemed less biased but also less precise (Table 2). When I combined bias and precision, conventional 2-dimensional distance sampling was more accurate, as would probably be expected given that it uses more data (precise perpendicular ranges to detected individuals, rather than presence–absence data at regularly spaced stations).

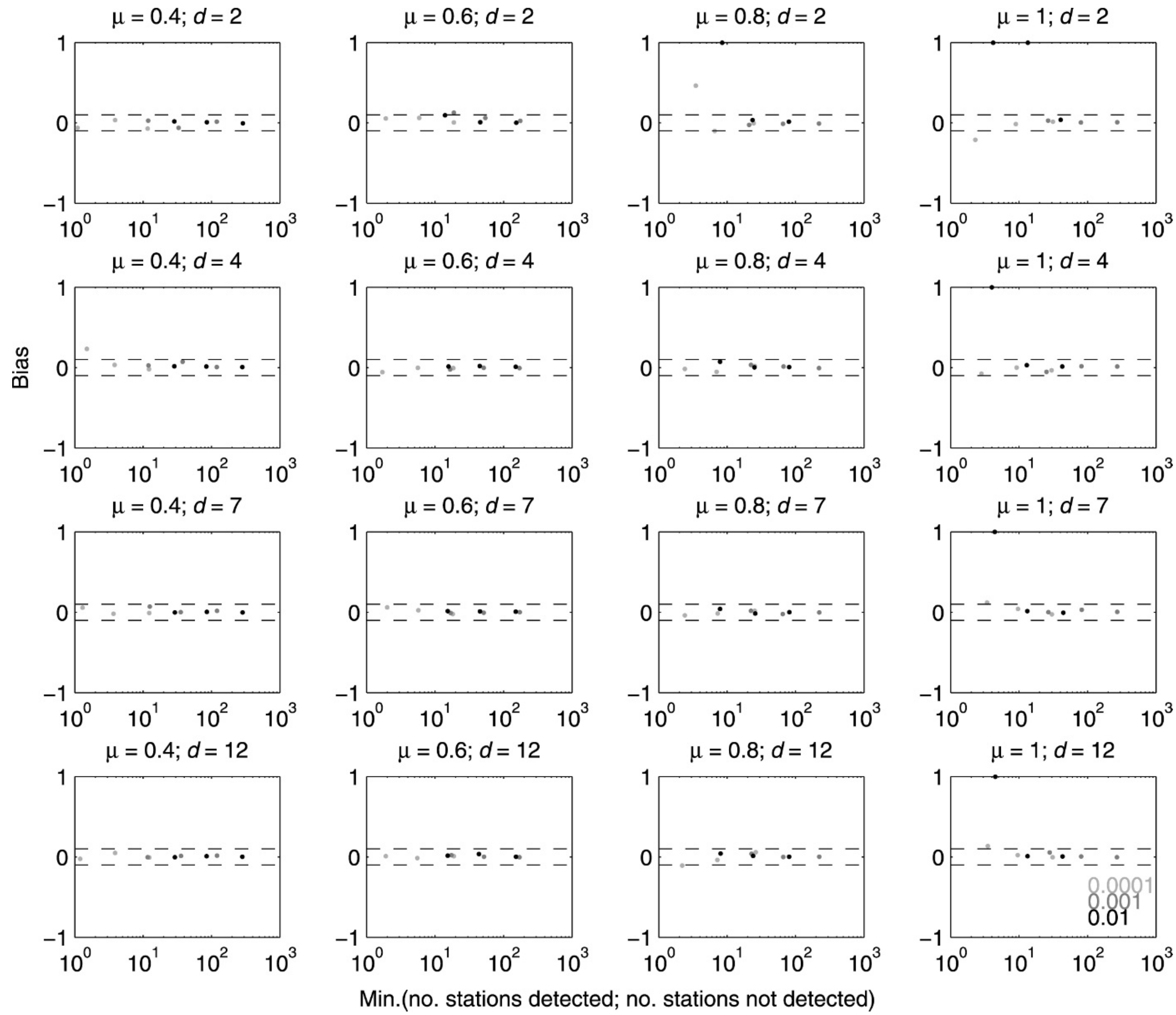

Figure 1. Both rate of vocalization (μ) and range of detection (r = 10 units) known. Mean proportional bias in estimates of density from 100 simulations [(estimated density − actual density) / actual density] plotted against minimum of the number of stations at which vocalizations were detected or not detected, as an indicator of information provided by the survey. There were no failures in these estimations. Shades indicate the density of vocalizers: black = 0.01, dark gray = 0.001, light gray = 0.0001 (giving approx. proportions of stations at which vocalizers were detected of 0.96, 0.27, and 0.03, respectively). Dashed lines indicate biases of 10%. Biases of >1.0 are represented as 1.0. d is distance between stations.

One-Dimensional Survey Using Real Data

We heard humpback whales at 148 of the Sargasso Sea stations (44.6%). When I assumed $\mu = 1.0$ (method C), there was no convergence in the estimation of r. Assuming no knowledge of r and μ (method D), r was estimated at 15.7 km (so $d/r = 0.37$), μ at 0.47, and density at 0.00162 whales/km^2. I used the parametric bootstrap to examine bias and precision in this estimate, carrying out 1,000 simulations (using model variant 1, variable inter-station intervals) with $\alpha = 0.00162/\text{km}^2$, $\mu = 0.47$, $d = 5.88$ km, CV(d) = 0.16, r = 15.7 km, and N = 332. These simulations suggested that the estimate of density had a coefficient of variation of about 0.68 and a positive bias of about 23%, roughly in accordance with model results (Fig. 4). The estimate of r = 15.7 km is consistent with previous estimates of ranges of hydrophone detection of humpback whale song, 9–32 km (summarized in Norris et al. 1999).

We heard sperm whales at 28 stations (8.4%). Assuming no knowledge of r and μ (method D), the estimates were r = 8.8 km, $\mu = 0.93$, and a density of 0.00039 groups of sperm whales/km^2. Parametric bootstrap simulations (as with the humpback whales) indicated a coefficient of variation of 0.37 for the estimate of density and a positive bias of 4%. When I assumed $\mu = 1.0$ and used method C, estimates were r = 8.0 km and a density of 0.00044 groups of sperm whales/km^2 (parametric bootstrap CV = 0.41; bias of −1%). These estimates of r are remarkably similar to those of effective strip widths from previous 2-dimensional acoustic surveys of sperm whales: 8.00 km (Leaper et al. 2000) and 7.99 km (Barlow and Taylor 2005). When

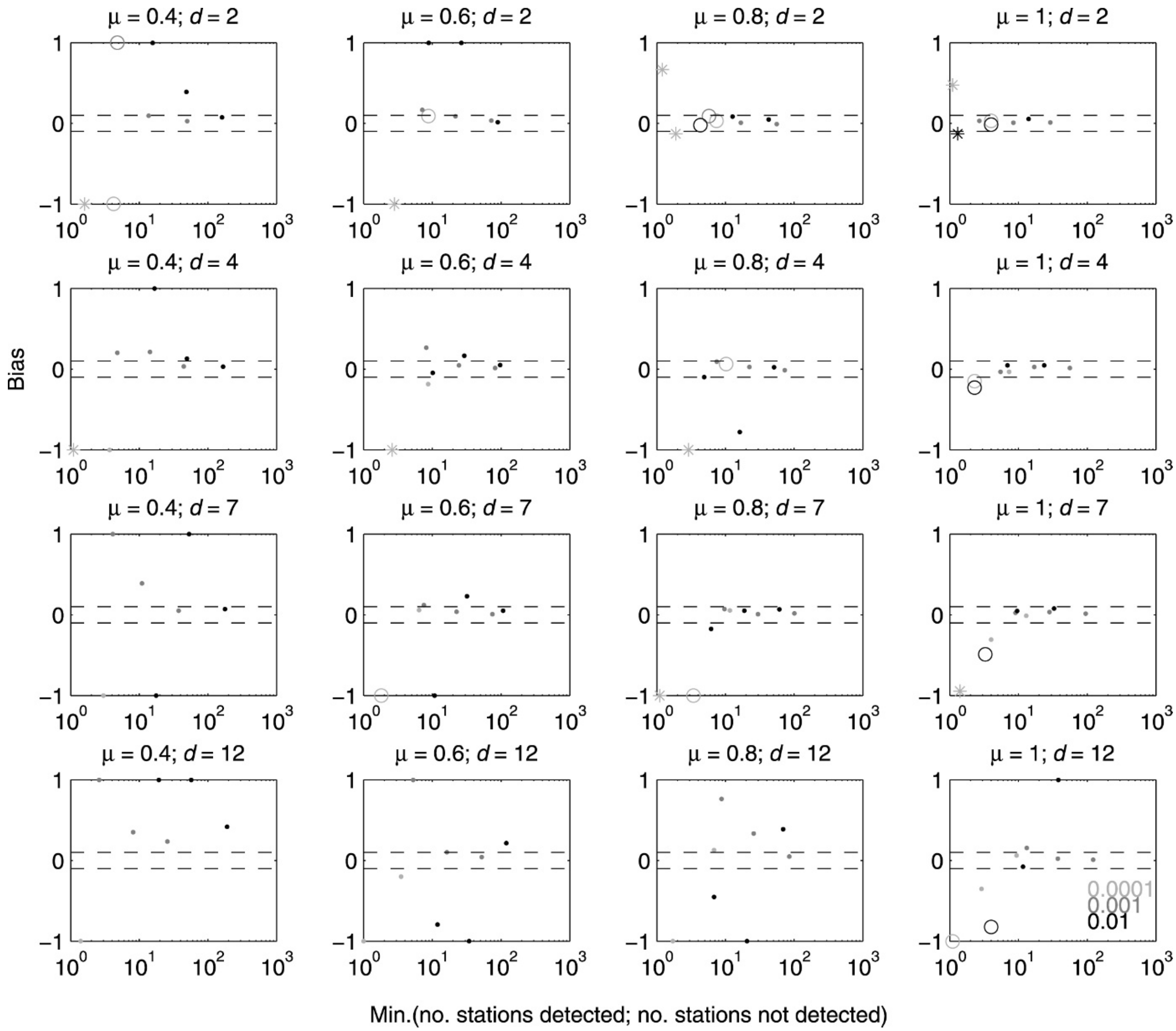

Figure 2. Range of detection known (r = 10 units). Mean proportional bias in estimates of density from 100 simulations [(estimated density − actual density) / actual density] plotted against the minimum of the number of stations at which vocalizations were detected or not detected following a station at which vocalizations were detected, as an indicator of the information provided by the survey. Proportion of estimates for which the methodology failed (because of failure to converge) is indicated by the symbol: · = no errors; o = 1–9 errors; * = 10–99 errors; no marker = 100 errors. Shades indicate density of vocalizers: black = 0.01, dark gray = 0.001, light gray = 0.0001 (giving approx. proportions of stations at which vocalizers were detected of 0.96, 0.27, and 0.03, respectively). Dashed lines indicate biases of 10%. Biases of >1.0 are represented as 1.0. d is distance between stations and μ is rate of vocalization.

corrected for the mean group size of sperm whales in the Sargasso Sea, about 12 animals (Gero 2005), the estimated sperm whale density of 0.0046 km^{-2} is within the range of those estimated from visual surveys of the species in other ocean areas (Whitehead 2002, Barlow and Taylor 2005).

DISCUSSION

My simulations suggest that one-dimensional acoustic surveys can provide estimates of the densities of wild animals with acceptable levels of bias under some conditions. The less we know, the more restrictive these conditions become.

Method A.—When both the range of detection and rate of vocalization were known, then method A seemed to work well under almost any conditions (except when vocalizations are detected at all or nearly all the stations) and was little affected by departures from the assumptions.

Method B.—When the range of detection was known but the rate of vocalization (μ) was not, then method B produced fairly unbiased estimates except when animals vocalized less than half the time, the inter-station interval was greater than the range of detection, or information was sparse because vocalizations were detected at almost all or almost none of the stations. When the detection range varied considerably between stations, a moderate positive bias was introduced.

Method C.—When the rate of vocalization (μ) was known and greater than about 0.7 but the range of detection

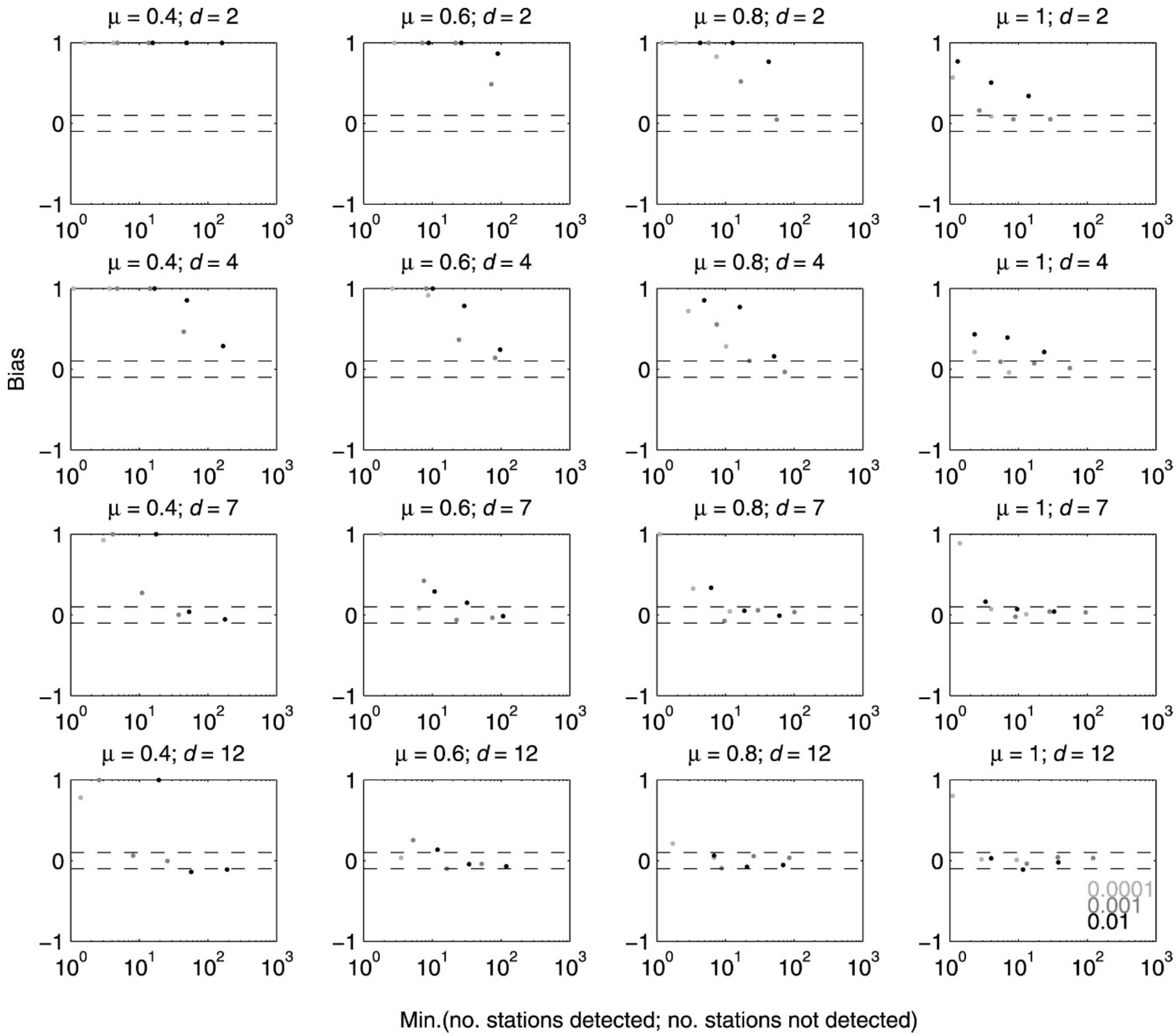

Figure 3. Rate of vocalization (μ) known. Mean proportional bias in estimates of density from 100 simulations [(estimated density − actual density) / actual density] plotted against the minimum of the number of stations at which vocalizations were detected or not detected following a station at which vocalizations were detected, as an indicator of the information provided by the survey. There were no failures in these estimations. Shades indicate the density of vocalizers: black = 0.01, dark gray = 0.001, light gray = 0.0001 (giving approx. proportions of stations at which vocalizers were detected of 0.96, 0.27, and 0.03, respectively). Dashed lines indicate biases of 10%. Biases of >1.0 are represented as 1.0. *d* is distance between stations. In the simulations, the real range of detection (*r*) was 10 units.

was unknown, then method C produced nearly unbiased estimates of density when information was sufficient and stations were separated by at least half the range of detection. Positive bias was introduced with substantial variability in the range of detection, and when animals actively avoided one another.

Method D.—With both the rate of vocalizations and range of detection to be estimated, stations needed to be spaced at 30–80% of the range of detection, and method D only worked consistently when rate of vocalizations was >0.7. As in Method C, substantial variability in the range of detection or animals avoiding one another introduced positive bias.

Thus the methods did seem to be useful in some circumstances, with the range of applicability being negatively related to the number of parameters that need to be estimated. In marginal circumstances, researchers should check for expected bias using parametric bootstrap simulation, although this assumes that the model used in the simulation is correct. The parametric bootstrap indicated little bias in the sperm whale density estimates and a moderate positive bias in the humpback density estimate, in accordance with expectations from the results of model simulations (Figs. 3, 4).

It is important to recognize that in the models evaluated, I assumed that probabilities that vocalizations were detected

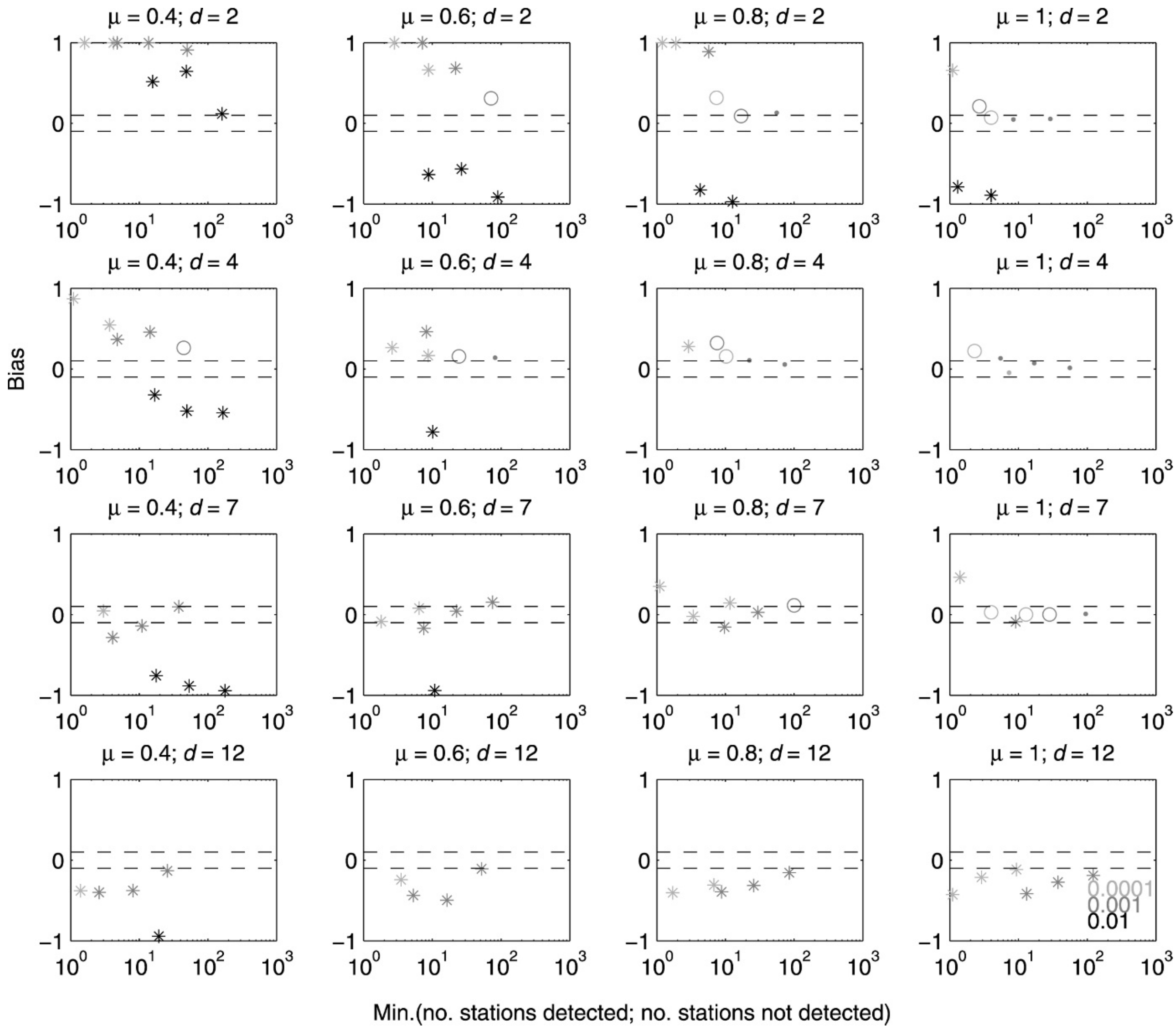

Figure 4. Neither rate of vocalization (μ) nor range of detection (*r*) known. Mean proportional bias in estimates of density from 100 simulations [(estimated density − actual density) / actual density] plotted against the minimum of the number of stations at which vocalizations were detected or not detected following a station at which vocalizations were detected, as an indicator of the information provided by the survey. Proportion of estimates for which the methodology failed (because of failure to converge) is indicated by the symbol: · = no errors; o = 1–9 errors; ∗ = 10–99 errors; no marker = 100 errors. Shades indicate density of vocalizers: black = 0.01, dark gray = 0.001, light gray = 0.0001 (giving approx. proportions of stations at which vocalizers were detected of 0.96, 0.27, and 0.03, respectively). Dashed lines indicate biases of 10%. Biases of >1.0 are represented as 1.0. *d* is distance between stations. In the simulations, the real value of *r* was 10 units.

from an individual within detection range were uncorrelated between successive stations. If animals may remain silent continuously for the time of passage over a few stations, then an additional correction should be applied for the continuously silent animals, in addition to the estimate of μ. The data needed to calculate such a correction will need to come from a study independent from the survey data.

The one-dimensional survey will be most useful with vocalizing animals, but it could be used with other modes of detection. For instance the method might also be useful with olfactory detection, for which range to the emitter is generally even harder to determine. The method seems to be only a little less accurate than conventional distance sampling when both are practicable. Although it could be used for visual detection, it is unlikely that it will be favored over conventional distance sampling with visual cues because the one-dimensional survey makes additional assumptions and requires omnidirectional observation around 360°, which is often not very practicable visually, and visual detection ranges are usually easily determined using range finders. Similarly in cases where good range estimates to vocalizers can be obtained (e.g., from towed hydrophone arrays in marine acoustic surveys; Lewis et al. 2007) there is little point in abandoning the many advantages of conventional distance sampling for a new method that makes additional assumptions.

Table 1. Effects of departures in assumptions of the methodology on the bias in estimates of density. Shown are mean estimates of density in 100 random runs. True density was 0.001.

Model variant[a]	Estimated density given: Known r and μ (method A)	Known r, estimate μ (method B)	Known μ, estimate r (method C)	Estimated r and μ (method D)
Standard	0.00100	0.00100	0.00100	0.00106
a) Variable d (SD = 20%d)	0.00099	0.00100	0.00102	0.00107
b) Variable r (SD = 20%r) by individual	0.00104	0.00103	0.00097	0.00101
c) Variable r (SD = 20%r) by station	0.00104	0.00114	0.00147	0.00129
d) Variable r (SD = 20%r) by individual/station pair	0.00105	0.00112	0.00137	0.00127
e) Increasing density along transect (from 0 to 2α)	0.00096	0.00092	0.00078	0.00078
f) Increasing density along transect (from 0.5α to 1.5α)	0.00098	0.00097	0.00096	0.00099
g) Individuals separated by $>r$	0.00104	0.00107	0.00120	0.00119
h) Individuals separated by $>r/2$	0.00102	0.00103	0.00105	0.00111
i) No individual isolated by $>5r$	0.00100	0.00100	0.00099	0.00107
j) Individual-specific μ	0.00099	0.00099	0.00102	0.00109

[a] r is the range of detection, d the interstation separation, and α the mean density.

However, for some organisms (e.g., some bats, birds, and cetaceans), and in some circumstances (e.g., night, fog, and thick vegetation), auditory or olfactory detection is more effective than sight, and ranges to animals cannot easily be measured. Although sounds and chemical cues have frequently been used as indices of abundance, their conversion into estimates of density or abundance has been rare, largely because of the challenges of estimating detection range, a requirement of conventional distance sampling. My one-dimensional survey methodology gives the potential for abundance or density to be obtained from such data, with no additional technical requirements in the field. The methodology can be applied directly to some archived data, such as sperm whale acoustic surveys (e.g., as described by Jaquet and Whitehead 1996), as long as the inter-station interval is suitable and fairly regular.

In planning future one-dimensional acoustic surveys, having selected the transect routes (see Buckland et al. 2001), the only important consideration is choosing the inter-station interval. My simulations suggest that about half the range of detection is suitable for all versions of the one-dimensional survey (also the min. inter-station interval for the technically more complex cartwheels method [which uses data on bearings to vocalizers] used by Gillespie 1997). Stations can be subsampled if they turn out to be too closely spaced.

Sometimes acoustic surveys operate in what is known as closing mode in which the transect is broken after some detections to investigate animals (e.g., Barlow and Taylor 2005). Density estimates can usually be made in these cases, although some care is needed with the denominators in the calculation of h (proportion of pairs of stations with vocalizations being detected at the first but not the second) and q (proportion of trios of stations with vocalizations being detected at the first but not the second or third). More serious problems will arise if the probability that the transect is broken is correlated with the probability that the vocalizations will be detected at the next station (the station that will be missed if the transect is broken), for instance in cases when transects are more often broken when vocalizations are louder.

No estimate of density or abundance has much value without some measure of precision and an idea of potential bias. In general, as with conventional distance sampling, the best estimates of precision are probably from comparisons of replicate, randomly or regularly placed transects (see Buckland et al. 2001). If the vocalization rate and range of detection are assumed similar on all transect lines, it is

Table 2. Mean bias (proportional deviation from true mean), precision (CV among estimates from different simulated data sets), and overall root-mean-square (RMS; square root of sum of squares of bias and precision) error for one-dimensional (method C) and 2-dimensional (using conventional distance-sampling) surveys of the same 1,000 simulated data sets.

	Form of simulation[a]	One-dimensional surveys	2-dimensional surveys
Proportional bias	Fixed r	+0.027	+0.039
	Variable r	+0.010	+0.085
Precision (CV)	Fixed r	0.276	0.224
	Variable r	0.283	0.250
Overall error (RMS)	Fixed r	0.277	0.227
	Variable r	0.283	0.264

[a] r is the range of detection.

probably optimal to make weighted averages of estimates of r and μ obtained for each transect line (using eqs 3–6) and then use these weighted averages to estimate density for each transect line (using eq 2).

An alternative method of estimating precision is the parametric bootstrap used above for the Sargasso transects, although it makes more assumptions. The parametric bootstrap also provides an estimate of bias that will be useful, especially when the technique is used close to the limits of its validity (as with the humpback whale estimate above).

Compared with the detailed development applied to distance-sampling methodology (e.g., Buckland et al. 2004), the simple analytical approximations I suggest are primitive. Although they seemed to work well in appropriate conditions, their performance, and especially their range of applicability, can undoubtedly be improved. Likelihood methods will almost certainly give better estimators of parameters and will allow relaxation of some assumptions. Likelihood methods may also use more of the data, if likelihood of the entire sequence station results (detected or not detected) can be calculated for a range of models and parameters. With likelihoods calculated, AIC or related measures will indicate the most appropriate model (Burnham and Anderson 2002). Bayesian techniques (Clark 2005) may be especially appropriate because often there will be useful prior knowledge about range of detectability (r), rate of vocalization (μ), and density. Incorporating this information using Bayesian methodology will improve estimates. Many of the other developments of conventional distance sampling including covariate models, temporal inferences, and spatial methods, could be applied to one-dimensional surveys (Buckland et al. 2004).

MANAGEMENT IMPLICATIONS

To assess status of wildlife populations and manage human impacts, we need estimates of absolute abundance. Absolute abundance is a prerequisite for assessment of the likelihood of stochastic extirpation, for assessment of the reduction of genetic diversity through the bottleneck effect, and to set removal quotas. For instance, 2 of the 5 International Union for Conservation of Nature criteria for Critically Endangered, Endangered, and Vulnerable species explicitly require absolute population estimates rather than trend data (International Union for Conservation of Nature 2008). Species that are hard to view because of their habitats or habits often lack absolute abundance estimates because of the difficulty of assessing range, and thus applying distance methods, when detection of individuals in surveys is not visual. The methods I developed give absolute estimates of abundance from some surveys in which ranges to detected individuals are not available. These methods will be particularly useful for species in which individuals are detected acoustically and may also be effective when detection is by chemical, or possibly electrical, signals.

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APPENDIX: ESTIMATING μ AND r FROM SEQUENCE DATA

K is the proportion of the area covered by listening at a station that was not covered by the listening at the previous, or subsequent, station. Then the probability that there are no new individuals detected at a station (i.e., individuals who were not within detection range of the previous station) is

$$e^{-aK\mu} \tag{A1}$$

where $a = \alpha\pi r^2$, the mean number of individuals expected to be detected at a station.

If x individuals are within detection range at the first station (present, not necessarily detected), then the probability that none of them are detected at the second is

$$= [K + (1 - K)(1 - \mu)]^x$$
$$= [1 - \mu + K\mu]^x \tag{A2}$$

The probability that if x individuals are within detection range at the first station and ≥ 1 are detected is

$$= 1 - (1 - \mu)^x \tag{A3}$$

Then, using the Poisson distribution, the probability that x individuals are within detection range at the first station is

$$= [1 - (1 - \mu)^x]\cdot a^x \cdot e^{-a}/x! \tag{A4}$$

Putting equations A1, A2, and A4 together, the probability that x individuals are within detection range at a station but no vocalizations were detected at the following station, is

$$= e^{-aK\mu}\cdot[1 - \mu + K\mu]^x\cdot[1 - (1 - \mu)^x]\cdot a^x\cdot e^{-a}/x!$$

Then, summing this over x, the probability that vocalizations are detected at a station but not at the following station is

$$h = e^{-aK\mu}\cdot \sum\nolimits_x [1 - \mu + K\mu]^x\cdot[1 - (1 - \mu)^x]\cdot a^x\cdot e^{-a}/x!$$
$$h = e^{-aK\mu}\cdot e^{-a}\cdot\left[e^{(1-\mu+K\mu)a} - e^{(1-\mu+K\mu)a(1-\mu)}\right]$$
$$h = e^{-a(K\mu+1-1+\mu-K\mu)}\cdot\left[1 - e^{-(1-\mu+K\mu)a\mu}\right]$$
$$h = e^{-a\mu}\cdot\left[1 - e^{-(1-\mu+K\mu)a\mu}\right]$$

So:

$$h = (1 - p)\cdot\left[1 - (1 - p)^{(1-\mu+K\mu)}\right]$$

where p is probability vocalizations are detected at a station ($p = 1 - \mathrm{e}^{-a\mu}$; from eq 1). Rearranging gives

$$1 - \mu + K\mu = \mathrm{Log}\left(1 - \frac{h}{1 - p}\right)\Big/\mathrm{Log}(1 - p)$$

and so

$$\mu = \frac{1 - \mathrm{Log}\left(1 - \frac{h}{1-p}\right)\Big/\mathrm{Log}(1 - p)}{1 - K} \tag{A5}$$

This can be used to estimate μ.

Next consider sequences of 3 stations with vocalizations detected at the first (S1) but not the second (S2) or third (S3). Let $q'(x,y,z)$ = (Probability x animals within detection range at S1) $\times$ (Probability ≥ 1 of x detected at S1) $\times$ (Probability y of the x were within detection range at S2) $\times$ (Probability z new individuals were within detection range at S2) $\times$ (Probability none of $y + z$ were detected at S2) $\times$ (Probability none of $y + z$ were detected at S3) $\times$ (Probability no new individuals were detected at S3):

$$\begin{aligned} q'(x, y, z) = {} & \frac{a^x\cdot e^{-a}}{x!}\cdot[1 - (1 - \mu)^x] \\ & \cdot(1 - K)^y\cdot K^{x-y}\cdot xCy\cdot\frac{(Ka)^z\cdot e^{-Ka}}{z!} \\ & \cdot(1 - \mu)^{y+z}\cdot[1 - \mu + K\mu]^{y+z}\cdot e^{-aK\mu} \end{aligned}$$

The terms of this expression come, respectively, from the Poisson distribution with parameter a, equation A3, the binomial distribution with parameter K, the Poisson distribution with parameter Ka, the binomial distribution with parameter $1 - \mu$, equation A2, and equation A1. Then the probability that vocalizations were detected at S1 but not S2 or S3 is:

$$q = \sum_x\sum_y\sum_z q'(x, y, z)$$

$$\begin{aligned} q = {} & \sum_x\sum_y \frac{a^x\cdot e^{-a}}{x!}\cdot[1 - (1 - \mu)^x]\cdot(1 - K)^y\cdot K^{x-y} \\ & \cdot xCy\cdot(1 - \mu)^y\cdot[1 - \mu + K\mu]^y\cdot e^{-Ka} \\ & \cdot e^{Ka(1-\mu)\cdot(1-\mu+K\mu)}\cdot e^{-aK\mu} \end{aligned}$$

$$\begin{aligned} q = {} & \sum_x \frac{a^x\cdot e^{-a}}{x!}\cdot[1 - (1 - \mu)^x]\cdot[K + (1 - K)\cdot(1 - \mu) \\ & \cdot(1 - \mu + K\mu)]^x\cdot e^{Ka[(1-\mu)\cdot(1-\mu+K\mu)-1-\mu]} \end{aligned}$$

$$\begin{aligned} q = {} & e^{-a+Ka[(1-\mu)\cdot(1-\mu+K\mu)-1-\mu]}\sum_x\frac{a^x}{x!} \\ & \cdot[1 - (1 - \mu)^x]\cdot\left[(1 - \mu + K\mu)^2 + \mu K(1 - K)\right]^x \end{aligned}$$

$$\begin{aligned} q = {} & e^{-a+Ka[(1-\mu)\cdot(1-\mu+K\mu)-1-\mu]} \\ & \cdot\left[e^{a[(1-\mu+K\mu)^z+\mu K(1-K)]} - e^{a(1-\mu)[(1-\mu+K\mu)^z+\mu K(1-K)]}\right] \end{aligned}$$

$$\begin{aligned} q = {} & e^{a\{-1+K[(1-\mu)\cdot(1-\mu+K\mu)-1-\mu]+[(1-\mu+K\mu)^z+\mu K(1-K)]\}} \\ & \cdot\left[1 - e^{-a\mu[(1-\mu+K\mu)^z+\mu K(1-K)]}\right] \end{aligned}$$

$$q = e^{a\mu(\mu-K\mu-2)}\cdot\left[1 - e^{-a\mu[(1-\mu+K\mu)^z+\mu K(1-K)]}\right] \tag{A6}$$

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